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*MIMICRY IN INSECTS.**

SHARING in the perplexity avowedly felt by many of my predecessors in this chair as to the choice of a subject for the annual address—perplexity arising rather from the redundancy than from the scarcity of entomological matter—I have been led to think, considering the wide reaching importance of the questions involved and the unmistakable interest shown in the recent discussion at two of our meetings, that some account of the mimetic relations existing among insects might not be out of place. Having for a considerable period devoted some attention to the matter, I propose to pass in review what has been placed on record; and if, in so doing, I traverse ground very familiar to most of us, my excuse must be the fascinating interest which attaches to the whole subject.

The application, by Henry Walter Bates, our lamented President, of the great principle of natural selection in elucidation of the mimicries found among insects† is too well known to require any detailed repetition here. It is sufficient to recall that, as the result of many years' experience in tropical South America, Bates established the facts that (1) among the abundant and conspicuous butterflies of the groups Da-

* Address of the President, Mr. Roland Trimen, F.R.S., before the Entomological Society of London, 1898.

† Trans. Linn. Soc., XXIII. (1862).

nainæ, Heliconiinæ, Acræinæ, and some Papilioninæ were found very much rarer mimicking forms, chiefly of the group Pierinæ, but partly belonging to other groups, and some even to the Heterocera, which, departing very widely from the aspect of their respective allies, imitated with more or less exactness the abundant species in question; (2) the numerous and showy Danainæ, etc., although of slow flight, did not appear to be molested by the usual insectivorous foes; and (3) the members of these unassailed tribes possessed malodorous juices not found in the mimicking forms or their allies. From these data he argued that the examination of these extraordinary resemblances was to be found in the great advantage it would be to species undefended by offensive secretions, and therefore palatable and much hunted down, to find escape in the disguise of species recognized and avoided as unpalatable; and traced the mimicries to the long-continued action of natural selection, perpetually weeding out by insectivorous agencies every occurring variation not in the direction of likeness to the protected forms, but as perpetually preserving, and so aiding the development by heredity, of every variation favorable to the attainment of the protective mimicry.

This sagacious application of the Darwinian theory in solution of one of the most difficult and baffling of the problems presented to zoologists was of the greatest service and encouragement to all students of evolution. I retain to-day the liveliest recollection of the delight I experienced in the perusal of a copy of Bates's Memoir received from himself; for his work was not that of the mere cabinet systematist, but came with all the force of face-to-face commune with the abounding life of the tropics.

Before two years had passed, Bates's explanation of mimicry was confirmed by his former companion in exploration, Alfred Russel Wallace, who, working with equal devotion in the Malayan Islands, had observed and was able to adduce a strictly analogous series of mimetic resemblances among Oriental butterflies, and gave his unreserved acceptance of the Batesian interpretation.* Such support from the cofounder with Darwin of the theory of natural selection, and from a naturalist of the widest experience in both Western and Eastern tropics, was of the greatest weight with evolutionists generally.

My own contribution to the subject was read to the Linnæan Society in March, 1868.† In the previous year I had made an entomological tour in Natal, and had enjoyed some precious opportunities of observing in nature several cases of mimicry between species not inhabiting the Cape Colony. There was no claim to originality in my paper; it simply rounded off the case by adding from Africa, the third great tropical region of the globe, a series of instances and observed facts confirmatory of those brought forward by Bates from the Neotropical, and by Wallace from the Oriental region. Of course, I had nothing like the extended field experiences of those great naturalists, and the African material then available was but scanty; but it so happened that perhaps the most striking and elaborate of all recorded cases of mimicry—that exhibited by the females of the *Merope* group of *Papilio*—had come under my personal observation in South Africa, and I was thus in a position to describe satisfactorily a wonderful illustration of the Batesian theory.‡

* Trans. Linn. Soc., XXV. (1864).

† Tran. Linn. Soc., XXVI. (1869).

‡ At various subsequent dates I was enabled, through the valuable aid of Mr. J. P. Mansel Weale and Colonel J. H. Bowker, to make known to science conclusive evidence of the species-identity of the three mimetic females of *Papilio cenea*, and of the pairing of the widely-differing sexes of that species. See Trans. Ent. Soc. Lond., 1874, p. 137, and 1881, p. 169; and 'South African Butterflies,' III., p. 254 (1889).

It will be remembered that Bates, in his memorable paper (*l. c.* p. 507), also brought to notice the very close resemblances, or apparent mimicries, which unquestionably exist between species belonging to different groups or subfamilies of protected distasteful butterflies themselves; but neither he nor Wallace felt able to give any explanation of these instances, which obviously differed very materially from the cases of mimicry of an unpalatable protected species by a palatable unprotected one. Not until 1879 was there any elucidation of this side of the matter, but in May of that year appeared in 'Kosmos,' Fritz Müller's notable paper on '*Ituna* and *Thyridia*,' which was translated by Professor Meldola, and printed in our 'Proceedings' for the same year (p. xx.). In this memoir Müller made the valuable suggestion that the advantage derivable from these resemblances between protected forms was the division between two species of the percentage of victims to the inexperience of young insectivorous enemies which every separate species, however well protected by distastefulness, must pay.

Professor Meldola not only brought forward and supported, with all his wonted grasp and acumen, F. Müller's daring interpretation of this phenomenon, but in 1882,* in a paper discussing the objections brought against Müller's view, made a distinct advance by showing how that view could justly be extended to explain the characteristic and peculiar prevalence of one type of coloring and marking throughout numbers of species in protected groups—so especially noticeable in the subfamilies Danainæ, Heliconiinæ and Acræinæ.

In 1887 was published† Professor Poulton's most interesting memoir entitled 'The Experimental Proof of the Protective Value of Colors and Markings in Insects in reference to their Vertebrate Enemies,' which dealt in great detail with the actual results of numerous experiments conducted by himself and other naturalists with the object of ascertaining to what extent highly conspicuous (almost always distasteful) larvæ and perfect insects are rejected or eaten by birds, lizards and frogs. The conclusions given at the close of this paper (pp. 266–267) cover a wide range in connection with the subject of warning coloration, and among them I would call special attention to No. 5, in which the author points out that "In the various species in which a conspicuous appearance is produced by color and marking, the same colors and patterns appear again and again repeated," and adds that "In this way the vertebrate enemies are only compelled to learn a few types of appearance, and the types themselves are of a kind which such enemies most easily learn." This generalization certainly had the merit of first detecting a great additional advantage derivable from the common aspect exhibited by a number of protected forms in the extended 'Müllerian' associations indicated by Professor Meldola; and it was applied by Wallace to the case of the Heliconiidæ in the comprehensive survey of warning coloration and mimicry generally given in 'Darwinism' (Ch. IX., pp. 232–267, 1889). We are further indebted to Professor Poulton for the discussion and summary of all extant data up to 1890 in his 'Colors of Animals,' a work which abounds in pregnant suggestion and indicates with justice and clearness how far the evidence forthcoming was valid and in what directions evidence still lacking should be sought.

Wallace well observed ('Darwinism,' p. 264) that "to set forth adequately the varied and surprising facts of mimicry would need a large and copiously illustrated volume; and no more interesting subject could be taken up by a naturalist who has

* Ann. and Mag. Nat. Hist. (5), X., pp. 417–425.
† Proc. Zool. Soc. Lond., 1887, pp. 191–274.

access to our great collections and can devote the necessary time to search out the many examples of mimicry that lie hidden in our museums." A work ostensibly of this character was issued in 1892–93, in two parts, from the pen of the late Dr. Erich Haase, under the title of 'Untersuchungen über die Mimicry auf Grundlage eines natürlichen Systems der Papilioniden;'* and last year an English translation of the second part was published and has quite recently been reviewed by Professor Poulton.† This treatise is of large quarto size, and the first part contains 120 pages and 6 colored plates, while the second extends to 158 pages and includes 8 colored plates. The first part‡ deals solely with the family Papilionidæ (*s. str.* = subfamily Papilioninæ) and principally with the great genus *Papilio* (*s. lat.*), which, on grounds of structure, system of markings, form of larvæ and pupæ and food-plants of larvæ, is divided into the three subgenera of *Pharmacophagus*, *Cosmodesmus* and *Papilio* (*s. str.*). With the utmost minuteness the species assigned to these groups, with their sexual, geographical or mimetic variations, are traced through the four zoological regions recognized by the author, and very elaborate analysis of markings is made in aid of arriving at their natural affinities from a phylogenetic point of view. Haase shows that in *Papilio* the models which are mimicked by other species of that great genus are always members of the *Pharmacophagus* group, or, as he calls them, 'Aristolochia-Butterflies'—whose larvæ feed on that tribe of plants, and which, as he contends, derive their offensive juices directly from the poisonous properties of their food in the early state.

In Part 2§ a lengthy account is given of the cases of mimicry occurring throughout the class of insects, and reference is also made to the few known instances in other classes of animals. The Lepidoptera occupy the bulk of the memoir, and, as in Part 1, a geographical order is followed, the mimicries in each of the four zoological regions being given under each of their respective families and genera, but in separated accounts of (firstly) models and (secondly) mimickers. In the 'Allgemeiner Theil,' which concludes the work and occupies about half of Part 2, there are sections treating of mimicry (*a*) within the limits of the old genus *Papilio* (in connection with Part 1), (*b*) between 'immune and non-immune' Lepidoptera, and (*c*) among 'immune' Lepidoptera themselves; followed by a consideration of objections to the theory of mimicry, and of mimicry as a part of protective adaptation to the environment.

While I regard Part 1 as a memoir of value, and as likely to prove serviceable to the student of a group so difficult to classify as the Papilioninæ, and while I recognize the great labor and research displayed throughout the work in the assembling of the accessible facts and data, I must reluctantly record my concurrence in Professor Poulton's severe criticism of the extremely unsatisfactory nature of the general treatment of the subject in Part 2. Apart from the cumbrous handling of the mass of details accumulated, the writer manifests such disregard of obvious difficulties, such unscientific haste in jumping at conclusions, and such inadequate recognition of what had been accomplished by previous investigators, that one can only regret that he ever entered on the speculative part of his work, and did not confine his energies to the better concentration and arrangement of the materials so assiduously collected.

Among recent contributions to the subject we shall, I think, all agree in assigning

* In Vol. III. of *Bibliotheca Zoologica* (Stuttgart).
† *Nature*, 4th and 11th November, 1897.
‡ *Entwurf eines natürlichen Systems der Papilioniden.*
§ Subtitle, 'Untersuchungen über die Mimicry.'

a high place to the memoirs with which Dr. F. A. Dixey has enriched our 'Transactions.' In 1894 he read before the Society his elaborate paper 'On the Phylogeny of the Pierinæ as illustrated by their Wing-markings and Geographical Distribution,' and took occasion to discuss the wide divergence from the primitive or typical pattern of the group caused by mimicry in such genera as *Euterpe*, *Pereute*, *Dismorphia*, etc. Adopting the Müllerian interpretation as expanded by Meldola, he proceeded to offer the original suggestion that, in the acquisition of closer resemblance between two or more protected forms, it was not necessary that in every instance the process of adaptation should lie solely in the imitation of one particular form as model, but that there might very well exist *mutual* convergence of the forms concerned, thus accelerating the attainment of the common beneficial resemblance. This 'reciprocal mimicry' the author further explained in a paper read in 1896 'On the Relation of Mimetic Patterns to the Original Form' (pp. 72–75), by a consideration of certain mimetic sets of Heliconii, Pierinæ and Papilioninæ, which present features and relations of pattern and coloring explicable apparently in no other way than by the hypothesis in question. This paper also gave a lucid demonstration, traced through corresponding series of existing forms of both mimetic and non-mimetic Pierinæ, of "the successive steps through which a complicated and practically perfect mimetic pattern could be evolved in simple and easy stages from a form presenting merely the ordinary aspect of its own genus," and further adduced reasons for holding that "it is not necessary that the forms between which mimicry originates should possess considerable initial resemblance." In his latest memoir, 'Mimetic Attraction,' read on May 5th last,* Dr. Dixey expanded a suggestion that he had previously (1896) made respecting divergent members of an inedible group, to point out—still from evidence in the Pierine subfamily to which he has devoted so much fruitful study—"how the process of gradual assimilation starting from one given point may take not one direction only, but several divergent paths at the same time," with the result that a more or less intimate mimetic relation was brought about with several protected forms of quite different affinities, though each connected in their coloring and aspect with some group of distasteful associates. He further set forth very fully the distinction which exists between the mimicry of inedible by edible forms, which could only be in one direction and was of advantage to the mimicker alone, and the assimilation among inedible forms themselves, where the mimetic attraction acts reciprocally, to the advantage of all participators.

Another of our Fellows, Colonel C. Swinhoe, distinguished for his wide and intimate knowledge of Oriental Lepidoptera, read before the Linnæan Society, in 1895, a most interesting paper 'On Mimicry in Butterflies of the genus *Hypolimnas*.'* In this memoir, as the author points out, a small group of wide-ranging mimetic insects is followed throughout its geographical distribution; and the process of mimetic modification is traced through the female, from the amazing instability of that sex of *H. bolina* (local form) in the Fiji Islands, where the male is stable and of the normal ancestral pattern and coloring, to the opposite extreme in Africa, where (with the exception of *H. misippus*) both sexes of the known allied forms of the genus are equally mimetic.† The singular contrast between

*Trans. Ent. Soc., Lond., 1897, p. 317.

*Linn. Soc. Journ. Zool., XXV., pp. 339–348.

† It should be noted that in the African *H. salmacis* and the Malagasy *H. dexithea* the sexes are alike and non-mimetic, and that therefore these species probably most closely approximate to the primitive appearance of the genus.

the numerous modifications of the female of the *Bolina* type, and the absolutely constant imitation of *Danais chrysippus* alone by the ♀ *H. misippus* is well brought out, and the different courses thus pursued by the respective females are shown to depend on the range, variation and abundance of the model that is mimicked. Colonel Swinhoe had previously (1887) published a good account of mimicry in Indian butterflies,* and in it made special reference to the remarkable series of close likenesses between species belonging to different subgenera of the great protected genus *Euplœa*.

So much prominence has naturally been given to the very conspicuous development of mimicry among the Lepidoptera that it is not uncommon to hear the matter spoken of as if limited to butterflies and moths, and even entomologists need to be reminded of the prevalence of the phenomenon among other orders of insects. The stinging Hymenoptera furnish the most numerous models to members of other orders, being closely mimicked by numerous Diptera, by many heterocerous Lepidoptera, by various Carabid, Heteromerous and Longicorn Coleoptera, and by some Hemiptera; while certain ants are well imitated by spiders. As regards Coleoptera mimicry is mainly found within the limits of the order itself—*e. g.*, Cicindelids by Heteromera and Longicorns, Carabids by Heteromera, Malacoderms by Longicorns, and Rhynchophora by Longicorns; but certain Cicindelid and Rhynchophorous beetles are closely copied by Orthoptera, belonging respectively to the genera *Condylodeira* and *Scepastus*. Lepidoptera do not seem to find mimickers beyond their own order, unless the case quoted by Haase† from E. Hartert, of the resemblance of a large Cicada to the Indian *Thaumantis aliris* (Morphinæ) be one of actual mimicry. Nor do Diptera appear to be models for imitation, except in the case of the hunting spiders, which mimick the Muscidæ they chase; although the neuropterous *Bittacus* certainly bears a strong likeness to Tipula, and may possibly find the advantage of that harmless aspect in approaching its prey. It cannot be denied that some of the interordinal mimicries are even more impressive and striking than those so notable among butterflies, the excellence of the superficial disguise of general outline, proportion of parts, coloring and markings being so great as to throw into obscurity the really vast structural discrepancies. Such cases as the imitation of the South American wasps of the genera *Polybia* and *Synœca* by moths of the genera *Sphecosoma* and *Myrmecopsis*,* of the Bornean sand-wasp *Mygnimia aviculus*, by the beetle *Coloborrhombus fasciatipennis*,† or of the Philippine tiger-beetle *Tricondyla* by the cricket *Condylodeira*, ‡ are absolute marvels of deception, all belonging to that special phase of mimicry where the obvious advantage to the unarmed mimic lies in being mistaken for the armed and formidable model.

As the Lepidoptera are at present the only order in which a very considerable number of mimetic relations have been observed, it may be of service to note here the various directions in which mimicry ramifies within the ordinal limits. The very large majority consists of cases where (*a*) Rhopalocera are copied by other Rhopalocera; and, taking the groups in succession, we find that (1) Danainæ (including Neotro-

* Journ. Bombay Nat. Hist. Soc., II., pp. 169–174.

† *Op. cit.*, II., p. 10. Haase (on p. 11) cites Brauer to the effect that the genus *Drepana* is mimicked by the neuropterous *Drepanopteryx*, which is stated to eed on Lepidoptera.

* See Haase, *l. c.*, II., p. 76, Pl. XIII.

† See Pryer, Trans. Ent. Soc., 1885, p. 369, Pl. X., who in the same place also figures another most striking case from Borneo, in which the hymenopterous *Triscolia patricialis* is mimicked by the lepidopterous *Scoliomima insignis*.

‡ See Bates, *l. c.*, p. 509.

pinæ) are mimicked by members of their own subfamily, by Satyrinæ, Heliconiinæ, Nymphalinæ, Erycinidæ, Pierinæ and Papilioninæ; (2) a few Morphinæ by Papilioninæ; (3) Heliconiinæ by Pierinæ; (4) Acræinæ by Nymphalinæ, Lycænidæ, Pierinæ, and Papilioninæ; (5) some Nymphalinæ, by members of their own subfamily; (6) Pierinæ by species of their own subfamily, and very rarely by Satyrinæ;* and (7) Papilioninæ by members of their own subfamily and by certain Pierinæ.

The next series is composed of those comparatively few instances where (*b*) Rhopalocera are imitated by Heterocera; and here it is found that (1) Danainæ (true, and Neotropinæ) are mimicked by Castniidæ, Chalcosiidæ (three different genera); Arctiidæ (two different genera), Dioptidæ (three different genera), and Geometræ (two different genera); (2) a few Acræinæ by Melameridæ (two different genera); (3) Papilioninæ by Castniidæ, Chalcosiidæ, and Arctiidæ.† Much rarer are the known cases of (*c*) mimicry of Heterocera by Rhopalocera; but (1) certain Uraniidæ are simulated by Papilioninæ; (2) Agaristidæ by Nymphalinæ; and (3) Lithosiidæ by Nymphalinæ. The mimicry of (*d*) Heterocera by Heterocera seems also to have been but seldom observed, but the cases recorded consist of (1) Agaristidæ by Liparidæ; (2) Melameridæ by Chalcosiidæ; (3) Geometridæ by Uraniidæ and Chalcosiidæ, and (4) Lithosiidæ by Agaristidæ.*

It will be seen that the foregoing enumeration includes not only the Batesian mimicries, but also those coming under the category of Müllerian associations of distasteful forms. To the latter class belong all cases occurring within the limits of the subfamilies Danainæ, Heliconiinæ and Acræinæ, and also many of those existing between species of one or more of those groups and certain Pierinæ and Papilioninæ, as well as (among moths) the Agaristidæ, some Lithosiidæ, and very probably others. It seems clear that, in the same circle of various species all approximating with more or less accuracy to one special type of coloration, marking and outline, there will often be found, in the larger and more comprehensive of such associations, both Batesian and Müllerian mimicries; this is, indeed, distinctly to be gathered from some of the cases tabulated by Bates himself, and has been lately well illustrated in the exceptionally rich Neotropical series of 'homœochromatic' forms brought before us by Mr. W. F. H. Blandford, among which were several of the actual specimens figured by Bates in illustrating his famous memoir. In the scarcely less opulent

* In the Oriental region *Delias* is mimicked by *Prioneris* and *Pieris*, and in the Ethiopian region *Mylothris* by *Pieris* and *Eronia*. An interesting case in support of the probable distastefulness of *Mylothris* is found in Madagascar, where the abundant *M. phileris* is mimicked by the very scarce *Elymnias masoura*, a Satyrine which is extremely divergent in coloring from all known members of its genus and subfamily.

† Col. Swinhoe informs me that the Pierine *Teracolus limbatus*— 'the southern form of *T. etrida*' —is accurately mimicked by the Geometrid moth, *Abraxas etridoides*. This case seems to support Col. Swinhoe's opinion (Proc. Ent. Soc. Lond., 1897, p. xxxvii.) that the species of *Teracolus* are inedible. I have noted (Proc. Zool. Soc. Lond., 1894, p. 21) another instance of marked resemblance to the females of the smaller East African *Teracoli* in the Satyrine, *Physcæneura pione*.

* There is some ground for suspecting *Acherontia atropos* to be a protected species. It has an apparent mimicker in Africa—its natural habitat—in the shape of another Sphingid of almost equal size, *Protoparce solani*, which, when seen at rest on tree trunks, I have, on more than one occasion, mistaken for the Death's Head. I do not know if any experiments as to the distastefulness of *Acherontia* have been made; but I incline to the belief that, if this moth is shunned by any insectivorous animals, such avoidance is more likely to be due to its squeaking powers and its threatening gesture, when irritated or alarmed, of suddenly elevating the robust and spiny fore legs. I know of no other moth that assumes this menacing attitude.

Oriental region (as Col. Swinhoe has pointed out in the paper above mentioned, and has more fully of late described to me) the same state of things is prevalent, extensive Müllerian inedible associations among (*e. g.*) the species of the three main groups into which the old genus *Euplœa* has been divided, being 'attended and surrounded' by numerous true mimics belonging to edible groups. The far poorer Ethiopian region has, to my knowledge, yielded as yet only a few series including both inedible and edible imitators; but in the group of which the Danaine *Amauris egialea* is the center there appears the exactly similar *Danais* (*Melinda*) *morgeni;* and in the same way the much-mimicked *Amauris echeria*, var., has in East Africa a protected companion in the female *Acrœa johnstoni*, while there is some reason for thinking that the widely-distributed *Acrœa encedon* is modified in resemblance to the dominant *Danais chrysippus*. Perhaps the most remarkable of these associations is that which surrounds the abundant and extremely conspicuous slow-flying diurnal Lithosiid moth, *Aletis helcita*. The apparently protected analogues of this insect are the closely similar Lithosiid *Phœagarista helcitoides* and Agaristid *Eusemia falkensteinii*, while the Batesian mimickers are found in the Nymphaline butterflies, *Euphœdra ruspina* and *E. eleus*, and the aberrant Lycœnid, *Liptena sanguinea*. Another point of interest in this last-named series is its great similarity in coloring and marking to that which is headed by *Danais chrysippus*, the differences being merely that in the *Aletis* set the red ground-color is brighter and the white spots in the black margins are larger; so that from the aspect of warning of distastefulness to enemies the two sets may be regarded as practically but one.

Among the Batesian mimicries in the Ethiopian region, I wish to revert more fully to the very striking and instructive case, already briefly referred to, presented by the females of the *Merope* group of the genus *Papilio*, because it has largely gained in interest by the increase of our knowledge in recent years. In 1867, when I wrote the paper above mentioned,* only three forms of the *Merope* group were known, *vid.:* the West African *P. merope*, the South African *P. cenea* (then regarded as not more than a variety of *P. merope*), and the Madagascar *P. meriones*. Of these the last-named alone had the sexes nearly alike, *vid.:* of a very pale yellow, margined with black in the forewings, and with the hind wings more or less black-marked and bearing conspicuous tails; each of the two continental species presenting not only the utmost disparity between the sexes, but also the singular phenomenon of a polymorphic female, invariably without tails, accurately mimicking two or three widely-differing species of Danainæ, and at the same time offering numerous linking variations. I was justified in considering that the Madagascar form should be regarded as retaining the ancestral condition of this group of *Papilio*, while the females of the continental forms had been profoundly modified in the mimetic directions specified; and I pointed to the costal black bar in the fore wings of the female *P. meriones* as possibly indicating the feature on which natural selection had been able to work, to the ultimate production of close imitation first of the lighter and at length of the darker Danainæ concerned.

It was startling to learn, in 1883, that a newly-discovered continental form of the group, *P. antinorii*, inhabiting Abyssinia, like the Madagascar *P. meriones*, had the sexes quite alike, except for the costal black bar in the female; while in 1889 there was described from the Comoro Islands a fifth and very distinct species, *P. humblœti*,

* Trans. Linn. Soc., XXVI.

in which the sexes resemble each other even more closely than in the Madagascar form, and which, therefore, in all probability exhibits a still more primitive condition.

The survival of the ancestral similarity of the sexes on the African mainland, so far from the Malagasy archipelago as Abyssinia, was a discovery of much importance; and the greatest interest was added to the whole case when, in 1890, Professor N. M. Kheil,* of Prague, described and figured two most remarkable new forms of the female *P. antinorii*. These females, given by the author as 'ab. *niavioides*' and 'ab. *ruspinæ*,' respectively, in coloring and pattern mimic *Amauris dominicanus* and *Danais chrysippus*, almost as closely as do the *hippocoonoides* and *trophonius* females of *P. cenea*, but yet retain on the hind wings the fully-developed tails possessed by the male and the unmodified female.† One would naturally suppose that these conspicuous appendages to the hind wings, never found in the Danaidæ, but so characteristic of many groups of *Papilio*, would have been among the first features to be lost in the process of assimilation to the Danaine models; and, as Professor Kheil mentioned in his paper, that the tails of the specimens of '*niavioides*' were injured, but had been restored in the figure, I felt a little doubtful about them, and ventured recently to address him on the subject. He most obligingly answered my inquiries, stating that the two forms of female were still in his possession, and that while the tails of the ab. *niavioides* were injured, as originally pointed out, those of the ab. *ruspinæ* were intact and are correctly delineated in Haase's figure, which—as well as that of *niavioides*—was drawn from the actual specimens, lent by Professor Kheil. It is to be noted that the tails are uniformly black, in accord with the broad hind margins, instead of being pale yellow with a short median streak of black, as in the female of the male coloration. Professor Kheil further informed me that the discoverer of these forms, the late Dr. A. Stecker, who collected at Lake Tana, brought together seven males, two females like the male, and one only of each mimetic form of female, and that he reported the male as very common, while the females seldom occurred.

This persistence in Abyssinia of the original female *P. antinorii*, side by side with two mimetic forms of the same sex retaining her outline of hind wings, but far divergent from her in advanced imitation of two very different Danainæ belonging to distinct genera, is strong confirmatory evidence of the view I advanced as to the development of the various tail-less mimetic African females of the group from the ordinary male-like type of female solely prevalent still in the Malagasy sub-region. From analogy with what occurs over so large an area of the rest of Africa, I confidently anticipate that we shall receive from Abyssinia intermediate gradations between the three known forms of the female *P. antinorii*; and as the dominant model, *Amauris echeria*, is represented in Abyssinia by the abundant and very closely allied *A. steckeri*, I should not be surprised to see another mimetic female of *P. antinorii* closely resembling the typical *P. cenea*. More than this, we may not unreasonably hope to discover, at some point in the wide territories between Abyssinia and Zanzibar, females of the *Merope* group exhibiting stages intermediate between long-tailed mimetic females of *P. antinorii* and entirely tail-less ones of *P. cenea*.

While dealing with this case, I would add that, until recently, of all the various tail-less continental females of this group known to me, the form *dionysos*—a rare phase of the West African *P. merope*—was the least modified as compared with the male,* for it

* 'Iris,' III., pp. 333-336.

†For colored figures in three forms of *P. antinorii*, ♀, see Haase, *l. c.* II., Pl. I.

*See Trans. Ent. Soc., Lond., 1874, p. 178.

possesses merely a trace of the wide black bar that in two other forms divides the pale ground color into perfectly separate subapical and inner marginal spaces in the fore wings, and the hind wings are ochre-yellow with a narrow black border.* Professor Poulton has, however, kindly shown me, in the Hope Collection of the Oxford University Museum, a much closer approximation to the masculine coloration in an extraordinary example of the female *P. cenea* from Zanzibar. In this female the transverse trace of black in the fore wings is even fainter than in the *dionysos* form, and the color of the wide pale spaces and hind marginal spots in all the wings is almost exactly of the pale creamy-yellowish tint of the male *P. cenea;* and on the under side, while the pale-yellowish of the fore wings is better divided by blackish than on the upper side, the coloring of the hind wings corresponds much more nearly to that of male than in any other female I have seen—the characteristic break in the submarginal brownish band being moreover very complete and wide. There can be no doubt that in this specimen we have a marked case of reversion to the original coloring of the female, but it is unaccompanied by any inclination towards the recovery of the lost tail of the hind wings.

Returning to the general aspects of the subject, it is of importance to consider more closely how the evidence stands in relation to (*a*) persecution by insectivorous foes; (*b*) possession of malodorous and distasteful juices by certain groups; (*c*) rejection or avoidance by foes of the insects provided with offensive juices, and (*d*) loss occasioned to distasteful species by the attacks of young and inexperienced enemies; for it is admittedly on the cooperation of these factors that the theory of mimicry depends.

(*a*) As regards the first point, the broad fact of insects generally constituting the food of countless devourers, vertebrate and invertebrate, is beyond dispute; immense and incessant persecution is universally at work. But when we proceed to examine this world-wide persecution more in detail, and to ask in what special directions it works, or what groups or species are the particular prey of certain groups or species of enemies, we very soon discover how little is exactly known. Birds, for instance, are such notorious and apparently indiscriminate insect-eaters, and some of them are so active and demonstrative in their hunting, that it seems but reasonable to regard them as the chief pursuers on the wing of the abundant and defenceless butterflies. Yet in the discussion which followed the reading of Dr. Dixey's last paper, above referred to, nothing was more noticeable than the very scanty testimony to such persecution on the part of birds that could be brought forward by the very competent well-travelled entomologists present. In fact, the poverty of observed cases of such attack has induced the opinion among some entomologists that birds very rarely chase butterflies at all, and the published expression of this view by Pryer, Skertchley, Piepers and other experienced collectors cannot be overlooked. But I am persuaded that in this instance, as in so many others where the life-history of animals is concerned, the dearth of evidence is due to the neglect of well-directed and sustained observation. Little can be gained by merely noting such cases as happen to force themselves on the collector's attention; the collector must resolutely set himself to search out and keep watch upon what really takes place. Considering that there is no record of any naturalist's having seriously taken up the investigation of this matter in the field, I think that very much positive evidence could hardly be expected, and that

*Hewitson (Exot. Butt., IV., Papilio XII., fig. 39) delineates an example in many respects intermediate between *dionysos* and *hippocoon*, but rather closer to the latter form as regards the fore wings.

what has been published goes far in the direction of proving that birds must still be reckoned among the principal enemies of butterflies. Belt's well-known note on the pair of Puff-birds that he watched for half-an-hour bringing various butterflies to feed their young is supported by E. Poeppig's observation* that in the forest it is easy to discover where a *Galbula's* favorite perch has been chosen, as the wings of large butterflies, whose bodies only have been eaten, strew the ground for several paces round about. Von Wied found a large 'Tagschmetterling' in the stomach of a *Bucco*, and E. Hartert butterflies in that of *Merops pusillus*; while E. L. Arnold saw *Terias hecabe* and *Papilio pammon* caught by birds in India.† Hahnel published in *Iris* (1890) the observation that in South America birds hunted Pierinæ more than any other group of butterflies, and often snapped up specimens close to him. Haase in Siam saw some Catopsiliæ (Pierinæ) and Hesperiidæ captured and eaten by sparrows. I have recorded Mrs. Barber's remarks that among the insects caught and brought to their nestlings by various Sun-birds at the Cape she often noticed *Pyrameis cardui*, and also Mr. Mansel Weale's note that *Tchitrea cristata* captures the male *Papilio cena*. Mr. T. Ayres, a very trustworthy ornithological observer, has remarked (in his notes in *The Ibis* on the habits of South African birds) that the King-hunter, *Ispidina natalensis*, feeds almost entirely on butterflies. Col. Swinhoe informs me that in India he has on several occasions seen *Merops viridis* catch and eat butterflies, and that he has also witnessed many cases of other birds pursuing them; while the common *Corvus splendens* was found greedily to devour any edible butterflies thrown to it. This evidence is supported by that kindly furnished to me by Mr. F. Lewis, of the Ceylon Forest Service, who has for many years been familiar with the ways of birds in the jungle, *vid.*: that he has seen *Merops viridis* and *M. philippinus* occasionally take small white and yellow butterflies (*Terias, spp.*), and the latter bee-eater and *M. swinhoii* frequently capture Catopsiliæ, especially when these butterflies are traveling in thousands along the river valleys. Mr. Lewis also gives *Buchanga leucopygialis* as a very active hunter of butterflies on the wing. In England I have noticed a swallow hunting one of the common 'Whites' (apparently *Pieris brassicæ*), and also three sparrows for some time chase and eventually capture a female *Epinephile janira*; while at the Cape I have seen *Fiscus collaris*, the common shrike of the colony, seize in succession several newly-emerged *Papilio lycæus* on the wing.

In Mr. Skertchley's paper, 'On Butterflies' Enemies,'* he gives a list (p. 485) of no fewer than twenty-three species of butterflies belonging to the different subfamilies, which he observed in Borneo with both hind wings mutilated in the same manner as if a piece had been bitten out while the insect was at rest; but this description of mutilation he attributes, not to the assaults of birds, but to those of lizards and perhaps small mammals. I see nothing, however, to lead us to conclude that birds do not attack butterflies when at rest, especially when settled on flowers, foliage, etc., with closed and erect or pendant wings; it is highly probable, indeed, that they would mark down a settling butterfly and make direct for it. It seems to me likely that most of the destruction of butterflies by birds is not effected by the difficult chase of these wavering and erratic or often very rapid flyers in the open, but is carried on mainly against the slow-flying bulkier females while engaged in depositing their ova, usually among the foliage of trees, un-

* Cited by Haase, l. c., II., p. 104.

† These three cases also cited by Haase, l. c.

* Ann. & Mag. Nat. Hist. (6) III., pp. 477–485 (1889).

dergrowth or herbage, where they would be almost unnoticed by the collectors. An equally, if not more, dangerous time for butterflies of both sexes is during courtship and pairing, when they are less on their guard than at any other period, and those actually paired (unless very well concealed by close resemblance of their under side to the immediate surroundings) have little chance of escape.* Colonel Swinhoe has mentioned to me that birds often do not seem inclined to take the trouble to give chase to flying butterflies, but sit merely watching them, and this is in support of the view that they more frequently adopt the easier plan of attacking them when feeding, settling or at rest. The frequency of the cases where mimicry is confined to the female points with some significance to the probability that persecution is more directed against that sex than against the male.

(*b*) The presence of malodorous juices in many insects is a matter of common observation, and is a protective property possessed by several entire groups, especially among the Lepidoptera and Coleoptera. There is abundant evidence as to the prevalence of these secretions, and among the Lepidoptera they are particularly developed in the butterflies of the groups Danainæ, Neotropinæ, Acræinæ and Heliconinæ, and also in some Papilioninæ, as well as in many moths of the groups Agaristidæ, Chalcosiidæ, Arctiidæ, Lithosiidæ, etc. The strength of the disagreeable odor emitted is in some species very great;† Seitz, for instance, mentioning that that the smell of the South American *Heliconius besckei* and *Eueides aliphera* extends over a radius of several paces, and Wood-Mason and De Nicéville testifying to the same effect as regards the Indian *Papilio philoxenus* and allied forms. When molested many of these offensively-smelling species exude drops of a yellow or whitish fluid which leave on anything they touch a stain and odor difficult to remove, as I have experienced in the case of the Mauritian *Euplœa euphone*, the South African Danainæ, and various South African Agaristidæ, Glaucopidæ and Arctiidæ.

The origin and manner of acquisition of these unsavory secretions have yet to be discovered; the suggestion (so much insisted on by Haase) that these juices are directly derived from those of similar quality in the food plants of the larvæ arising from the long-known circumstance that some of the food plants of species in the protected groups are of an acrid or poisonous character, such as (*e.g.*) Asclepiads in the case of many Danainæ, and Aristolochia in that of the inedible forms of Papilioninæ. No doubt, too, the fact that the unpleasant qualities are very often fully developed in the larvæ of the distasteful species—as I have found with *Danais chrysippus* and various Acrææ—lends some weight to the suggestion; but at present nothing approaching sufficient data can be brought forward respecting the actual food plants to which the protected groups, in contrast to the unprotected, are thought to be restricted. It cannot be gainsaid, as Professor Poulton has pointed out,* that the food plants of many of the distasteful European moths do not belong to any poisonous or acrid category; and his own and Mr. Latter's papers on *Dicranura vinula* alone amply demonstrate what powerful acids can be elaborated by a larva which finds its food in such innocuous plants as poplar and willow. The supposed direct derivation of the nauseous juices from the plants consumed is thus plainly a matter that awaits

* It is not improbably in these circumstances that the imperfectly mimetic but still 'warning' under side of the male in *Perrhybris* becomes specially serviceable (*Cf.* Dixey, Trans. Ent. Soc. 1896, p. 71).

† Cited by Haase, *l. c.*, II., p. 101.

* Proc. Zool. Soc. Lond., 1887, pp. 198, etc., and *Nature*, 4th Nov., 1897, p. 3.

investigation from both biological and chemical standpoints.

(*c*) The avoidance or rejection as food by insectivorous animals of the insect possessing malodorous or distasteful juices no longer rests merely on the negative evidence given by Bates, Wallace, Belt and other competent observers, to the effect that in nature such distasteful forms are habitually neglected and unmolested; there is now much positive experimental evidence as to the manifest avoidance or disgust with which such species are left untouched, or thrown aside after tasting, when offered to domesticated or captive vertebrate animals that devour ordinary insects with avidity. The numerous experiments of this kind recorded by Butler, Jenner Weir, Weismann, Poulton and Lloyd-Morgan, as regards both larvæ and imagos of European species, are supported by a few made by Belt with Heliconiinæ in Central America, by D'Urban and myself with Danainæ and Acræinæ * in South Africa, and by Haase with Danainæ in Singapore.

It is manifest, of course, that even the most distasteful forms cannot enjoy complete immunity from persecution; in ordinary circumstances they are doubtless mainly kept down by parasitic insects, † and during any scarcity of more palatable prey it is certain that they will be devoured *faute de mieux* by vertebrates and invertebrates alike. To the latter condition are perhaps due such cases as Distant's ‡ note of the orthopterous *Hemisaga* devouring an imago of *Danais chrysippus*; Col. Yerbury's * observation that in Ceylon *Euplœa core* and *Delias eucharis* were largely taken by a Mantis, and *Danais limniace* by two kinds of Asilidæ; and Belt's remark that a flower-frequenting spider captured Heliconiidæ.

(*d*) As regards the important point whether the protected forms have to suffer a certain percentage of loss from the attacks of young and inexperienced birds and animals, it must be admitted that the evidence at present forthcoming is exceedingly scanty; and I have long felt considerable doubt as to the sufficiency of this factor to account for the mimetic resemblances, often remarkably close, between members of associated protective groups. But on reviewing carefully the recorded observations which appear to bear on the question, I have found reason to think that there is enough support to justify the provisional acceptance of the Müllerian explanation. We have, in the first place, Fritz Müller's own capture of Heliconii and Acræinæ with a notched piece bitten out of the wings, and Distant's (*l. c.*, p. 65) of a *Danais chrysippus* whose wings had been bitten unsymetrically, apparently by a bird. Then there is the significant record of Skertchley (*l. c.*, p. 485) who, among twenty-three species of Bornean butterflies taken with both hind wings mutilated in the same manner, notes no less than four Danainæ, *vid.*, *Hestia lynceus*, *H. leuconœ*, *Ideopsis daos* and *Euplœa midamus*. Moreover, it is very remarkable that several of those entomologists who have specially emphasized the small part played by birds in attacking butterflies mention, among the few cases of such attack as they witnessed, instances of protected forms being assailed, Sir G. Hampson † remarking that in south India the Euplœæ and Danaids were caught as often

* De Nicéville (Butt. Ind., etc., I., p., 318) notes that *Acræa violæ* was the only butterfly rejected by all the species of Mantidæ which he offered various butterflies.

† C. V. Riley (apud Haase, *l. c.*, II., p. 47) found that a dipterous parasite was very prevalent in the larvæ of *Danais archippus*, often destroying a whole brood.

‡ Nat. in Transvaal, p. 65 (1889).

* Proc. Ent. Soc. Lond., 1897, p. xl.

† Proc. Ent. Soc. Lond., 1897, p. xxxvii.

as any others, and M. Piepers* that in two of the four cases which he had seen in Sumatra and Java the species seized were Euplœæ.

The question underlying this is manifestly whether insect-eating animals have an instinctive inherited discernment of what species are unfit for food, or whether, on the contrary, each individual has to acquire this necessary knowledge by personal experience, aided in some vertebrate groups by parental guidance. So numerous and so marvelous are the instinctive or congenital activities of animals—especially in the insect world, where past experience or parental instruction is almost always non-existent—that there has been a very general disposition on the part of naturalists to incline to the former view in a matter so all-important as suitable food. Yet, so far as experiment has hitherto gone in this direction, there seems good ground for holding that—at any rate in such specially insectivorous vertebrate groups as birds, lizards and frogs—the young possess no such hereditary faculty of discrimination, but have to discover individually what to avoid. This appears not only from Mr. Jenner Weir's and especially Professor Poulton's careful and often-repeated experiments with lizards and frogs,† but also from Professor Lloyd Morgan's study‡ of newly-hatched birds of different orders, which indicates clearly with what complete want of discrimination every object of suitable size is at first pecked and tasted, but how soon experience tells and is acted upon. Professor Lloyd Morgan made special trial of these young birds with many distasteful insects and their larvæ, and states in conclusion (*l. c.*, p. 43) that he did not find a single instance of instinctive avoidance, but that the result of his observations is that "in the absence of parental guidance the young birds have to learn for themselves what is good to eat and what is distasteful, and have no instinctive aversions."

In concluding what I feel to be a very incomplete outline of what has been done in this most important branch of zoological research, I cannot refrain from expressing the gratification I find in noting how by far the chief part in the investigations pursued and in the deductions derived from them has from the outset been borne by Fellows of this Society. It is work on which we may with justice be congratulated, and which should encourage perseverance in the same and kindred lines of inquiry.

Here, as in many other biological researches, it cannot be too strongly insisted on that no result of lasting value can be hoped for without resort to the living animals among all the natural conditions and surroundings. It was not a stay-at-home theorist, familiar only with the dried specimens of the cabinet, that detected the meaning of mimicry and gave to science a rational explanation of the mystery, but an ardent explorer and naturalist, who devoted many of the best years of his life to field-work in tropical lands. I am the last to undervalue the knowledge of the systematist, which is absolutely indispensable to all intelligible record, and I fully recognize that no naturalist can be properly equipped for his work without a fair amount of systematic training; but philosophical discovery in any direction such as we are now considering can never be truly advanced without unflagging observation and experiment among organisms living in their environment. How, but by the closest and most exact attention to the entire life-history of animals in their native haunts can we expect to deal satisfactorily with such questions as this of mimicry, of protective resemblances generally, of seasonal dimor-

* Report of Intern. Zool. Congress, III. (Leyden, 1895), p. 460.

† See Proc. Zool. Soc. Lond., 1887, pp. 191, etc.

‡ 'Habit and Instinct,' pp. 29–58.

phism, sexual selection, local variation, and the like? Admitting gratefully the good work of this kind which has been carried on in Europe, and especially in our own country, one cannot but regret that from tropical regions, where alone the abundance, complexity and incessant activity of life afford full prospect of the adequate reward of such research, we have little more than isolated notes and unconnected and incomplete observations, mere indications—precious as they are—of the rich harvest that lies unreaped for lack of resident workers devoted to the task.

It is on this account that I earnestly renew the plea, put forward from this chair on the 5th of May last, for the establishment, in tropical countries, of Biological Stations for the study of the terrestrial fauna; where, as in the existing Marine Biological Stations, naturalists could follow, during a succession of seasons, special lines of observation and experiment under favorable conditions of laboratory and other equipment, free from the hindrances and distractions of ordinary collecting travel, and with all the advantages of mutual help and encouragement. The living expenses, for men of the simple tastes of the naturalist, would not be great; and I feel certain that, with the increasing facilities for swift transport, it would not be long before many students of biology would embrace the opportunity so provided for the effectual prosecution of researches of the utmost value to science.

WILLIAM A. ROGERS.

PROFESSOR WILLIAM A. ROGERS was born at Waterford, Connecticut, November 13, 1832, and died at Waterville, Maine, March 1, 1898. His boyhood was spent for the most part in the interior of New York State, in the villages of DeRuyter and Alfred, where he received his preparation for college. In 1853 he entered Brown University, from which he was graduated in 1857. Before graduation he had already begun his career as a teacher in a classical academy, and immediately after taking his first degree he was appointed tutor in the academy at Alfred, N. Y., from which he had gone forth a few years previously as an exceptionally successful student. In 1859 he was advanced to the professorship of mathematics and astronomy in Alfred University, an institution under the care of the Baptist denomination, of which Professor Rogers was an ardent member throughout his life. This position he held eleven years, though absent part of this time for several specific purposes. Among these absences one was devoted to a year of study in the Harvard College observatory; six months were occupied in work as an assistant in the same place; fourteen months were given to service in the navy during the Civil War; and nearly a year was given to the study of mechanics in the Sheffield Scientific School at New Haven.

In 1870 Professor Rogers severed his connection with Alfred University for the purpose of becoming an assistant in the astronomical observatory at Harvard, and in 1875 he was here made assistant professor of astronomy. This position he retained until 1886, when he accepted the chair of physics and astronomy at Colby University, Waterville, Maine. Here the last dozen years of his life were spent; but had he lived a month longer he would have resumed his connection with Alfred University, where a new physical laboratory is now in process of erection. The building was planned by him in 1897, and on the occasion of the laying of the cornerstone, June 23, 1897, Professor Rogers delivered the dedicatory address. His resignation had already been offered to the Trustees of Colby University, to take effect April 1, 1898.

During the sixty-five years of his busy